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Biomass and nutrient allocation as a function of stem bending of mutamba seedlings

Alocação de biomassa e nutrientes em mudas de mutamba em função de flexões caulinares

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ABSTRACT

The use of hardening or acclimatization processes in woody species seedlings has shown contradictory results in post-planting mortality. The hardening or acclimatization of woody species seedlings via mechanical treatment has resulted in differentiated nutritional allocation among plant tissues. The objective of this study was to test the effect of daily stem bending frequencies (zero, 10, 20, or 40 bends) on macronutrient allocation in *Guazuma ulmifolia* seedlings, using a randomized block design with five replicates of seven seedlings. The treatments tested did not show evidence of stress induction in seedlings when measured by the electrolyte leakage test in root tissues, but increased calcium and magnesium levels in the stem. The use of 10 daily stem bends resulted in an increase in nitrogen concentration in stem tissues, while phosphorus concentration increased in both the stem and roots. The imposition of 10 or 20 daily stem bends resulted in a reduction in potassium concentration in the roots, as well as an increase in calcium and magnesium levels in the stem. Due to the pioneering nature of the species and its ability to acclimatize mechanically, hardened mutamba seedlings with stem bends deserve to be tested in revegetation projects.

KEYWORDS: Indirect stress assessment. Nursery techniques. Electrolyte loss test. Seedling hardening.

RESUMO

O uso de processos de rustificação ou aclimatação em mudas de espécies lenhosas tem apresentado resultados contraditórios na mortalidade pós plantio. A nutrição mineral das mudas afeta a alocação de biomassa para os vários componentes acima e abaixo do solo. A rustificação ou aclimatação em mudas de espécies lenhosas via tratamento mecânico tem resultado em alocação nutricional diferenciada entre os tecidos vegetais. O ensaio objetivou testar o efeito de frequências de flexões caulinares diárias (zero, 10, 20 ou 40 flexões) na alocação de macronutrientes em mudas de *Guazuma ulmifolia*, em delineamento experimental de blocos casualizados, com cinco repetições de sete mudas. Os tratamentos testados não evidenciaram indução de estresse nas mudas quando aferido pelo teste do extravasamento de eletrólitos em tecidos radiculares, mas aumentaram os teores de cálcio e magnésio do caule. O uso de 10 flexões caulinares diárias resultou em aumento da concentração de nitrogênio nos tecidos do caule, enquanto a concentração de fósforo aumentou tanto no caule como nas raízes. A imposição de 10 ou 20 flexões caulinares diárias proporcionaram redução na concentração de potássio nas raízes, assim como um aumento dos teores de cálcio e magnésio no caule. Devido ao aspecto pioneiro da espécie e sua capacidade de aclimatação mecânica, mudas de mutamba rustificadas com flexões caulinares merecem serem testadas em projetos de revegetação.

PALAVRAS-CHAVE: Avaliação indireta de estresse. Teste da perda de eletrólitos. Técnicas de viveiro. Rustificação de mudas.

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INTRODUCTION

The study of nutrient allocation in woody species tissues is important for understanding life strategies and their success in dispersal, as they influence competitive capacity (LARCHER 2006). Inadequate mineral nutrition during seedling production has been identified as a limiting factor for growth and successful establishment of forest stands (OLIET et al. 2009).

Plant mineral nutrition affects the allocation of biomass in the various plant components above and below ground, aiming to maintain metabolism and survival (QI et al. 2019). The allocation of nutrients in terrestrial plants has been described through the preferential distribution of biomass in their various organs.

When stems bend or are damaged, vascular tissues responsible for water transport can rupture, potentially leading to reduced nutrient absorption and distribution. This, combined with morphophysiological changes in the root system, can result in nutritional deficiencies, especially in areas furthest from the point of stress perceived in the stem (LIU et al. 2023).

The induction of hardiness or acclimatization in the production of woody species seedlings aims to alter plant growth patterns (SAMPATHKUMAR et al. 2014). Mechanical manipulations in the nursery during propagation generally induce morphometric changes resulting from turgor pressure in the longitudinal direction with greater radial growth rather than longitudinal growth, as it alters the orientation of the microtubules and microfibrils of the cellulose in the primary cell wall and cytoplasm (LOPEZ et al. 2014). In turn, growth patterns in woody species seedlings have been correlated with post-planting survival (VOLKWEIS et al. 2020).

The hardening-off or acclimatization process is characterized by the use of nursery practices aimed at increasing tolerance to post-planting abiotic stresses (HEBERLE et al. 2018) through mechanical manipulations, changes in fertilization and irrigation dosages, and the application of plant growth regulators.

Hardening or acclimatization induces physiological, anatomical, or morphological adjustments in plants that improve performance or survival in response to environmental or stressful changes. The mechanical strength of the stem depends on carbohydrates, including non-structural and structural carbohydrates, mainly lignin and cellulose (ZHANG et al. 2014). The induction of hardening or acclimatization through stem bending can induce stress, resulting in differentiated nutritional allocation between aerial and root tissues (PUIJALON et al. 2007).

Guazuma ulmifolia Lamarck is a semi-deciduous, heliophytic, pioneer, calcifier tree species, indicative of mesotrophic soils (CARVALHO 2007), used in energy plantations for charcoal production and in the revegetation of degraded areas (PAIVA SOBRINHO & SIQUEIRA 2008). The species is common on the edges of cerradão woodland and even in the Pantanal or on the banks of small watercourses. It is resistant to light frosts and does not tolerate waterlogged soils (DURIGAN et al. 2002). Ten months after germination, mutamba seedlings showed acclimatization of the photochemical apparatus independent of the light environment in clearings or understory (SOUZA et al. 2010).

The species has great pharmacological and medicinal diversity due to its therapeutic properties (SILVA et al. 2020). Therefore, it accumulates primary and secondary metabolites, which act as signaling molecules to increase the expression of genes that confer protection against environmental stresses (RAMAKRISHNA & RAVISHANKAR 2011). The species is also characterized by active ingredients used to combat parasites such as *Leishmania brasiliensis*, *Leishmania infantum*, and *Trypanosoma cruzi* (CALIXTO JÚNIOR et al. 2016) and as an alternative treatment against HIV in Brazil (GOUVEIA 2018) and Venezuela (SINGER 2018).

Under abiotic stress, a plant's ability and efficiency in reconfiguring various metabolic networks are decisive factors in its acclimatization and survival, and involve the differentiated absorption of essential nutrients. Therefore, recognizing changes in nutrient absorption and accumulation patterns is important for understanding developmental processes and the chemical signaling that these processes can promote in response to stressful conditions.

Given the above, the objective of this study was to quantify the effect of the frequency of stem bending on the allocation of macronutrients in the stem and roots during the propagation of *G. ulmifolia*.

MATERIALS AND METHODS

The test was conducted in a shade house (50%) using *G. ulmifolia* seedlings produced from seeds collected at the nursery in Foz do Iguaçu, Paraná, located near the coordinates 24º 33' 22” S and 54º 03' 24” W.

The experiment followed a randomized block design with four frequencies of daily stem bending with five repetitions of seven seedlings each, totaling two hundred and eighty seedlings.

The seedlings, 90 days after sowing (DAS), were subjected to four daily frequencies of stem bending (zero, 10, 20, or 40 bends) according to VOLKWEIS et al. (2014). The treatments were applied for 30 days, during which all seedlings were irrigated to saturation once a day in the morning.

The seedlings resulted from sowing and procedures used in that nursery using commercial Humusfértil – Florestal® commercial substrate composed of pine bark, substrate sand, vermicompost, and vermiculite with the addition of Osmocote® 14-14-14, accompanied by fertilization with NPK 10-10-10 every 15 days for three months after sowing.

Before applying the treatments, the morphometry of the seedlings was characterized in terms of height and collar diameter, which were used to calculate the robustness index (ratio between height and collar diameter), and the number of leaves was counted. Additionally, the chlorophyll index was determined using a chlorophyll meter (SPAD 502 Minolta®) on leaves located in the middle third of the foliage.

After application of the treatments, seedlings aged 120 days after sowing were evaluated for root electrolyte extraction (REE), and the levels and contents of N, P, K, Ca, and Mg in stem and root tissues.

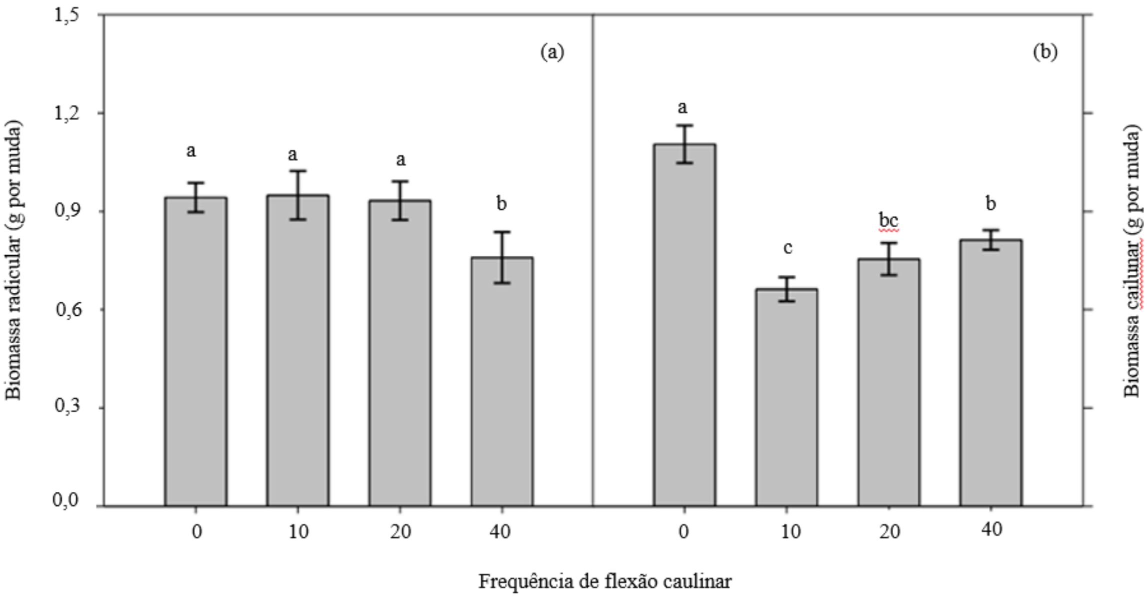
The REE test was determined according to the methodology of WILNER (1955), while macronutrients were determined using sulfuric digestion for N and nitro-perchloric digestion for K, Ca, Mg, and P, as described by LANA et al. (2010). In addition, the biomass of aerial and root tissues was determined by drying in an oven with air circulation at 65ºC for 72 hours.

The data were checked for normal distribution of residuals using the Shapiro-Wilk test, for homogeneity of variances using the Brown-Forsythe test, and subjected to analysis of variance using SigmaPlot 12.0 (SIGMAPLOT 2011). When significant differences existed, the means were compared using Tukey's test at a 5% probability of error.

RESULTS AND DISCUSSION

Morphometric analysis of the seedlings before treatment application indicated an average height of 20.1 cm and collar diameter of 2.8 mm, containing six leaves with an average of 28.8 SPAD units and a robustness index of 7.2, indicative of thin seedlings (AVELINO et al. 2021). The robustness index reveals the balance of growth between aerial and root tissues. The lower the robustness index value, the better the quality of the seedling, with a higher probability of survival and establishment after planting (CARGNELUTTI FILHO et al. 2018).

After 30 days of applying stem bending, it was observed that *G. ulmifolia* seedlings had a reduction in biomass accumulation in the root system with 40 bends per day, while lower intensities did not alter biomass allocation in the organ (Figure 1a). In the stem tissues, a significant reduction in biomass was observed in relation to non-bent seedlings, with the lowest values in seedlings that received 10 and 20 daily bends (Figure 1b).



Averages not followed by the same lowercase letter differ significantly from each other, according to the Tukey test, at a 5% probability of error.

Figure 1. Root biomass (a) and aerial biomass - stem plus leaves - (b) in seedlings of *G. ulmifolia* as a function of the frequency of stem bending.

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The analysis of the stressful effect of stem bending treatments was estimated by the electrolyte extrusion (REE) test in root tissues (GE et al. 2014). The interpretation of the results indicated an increase in electrolyte extrusion ($P<0.05$) in seedlings subjected to 40 daily stem bends (35.1%) compared to those obtained in control treatment seedlings (21.0%), signaling increased stress. The REE test values detected in seedlings subjected to frequencies of 10 (28.3%) and 20 (23.3%) stem bends suggest that those treatments did not induce stress, as they were similar to those observed in the control treatment. The REE test estimates the integrity and selectivity of root system cell membranes (KOVALESKI & GROSSMAN 2021) and is characterized by being a rapid indicator of stressful conditions.

The nitrogen content (N) content in the stems of *G. ulmifolia* seedlings (Table 1) increased ($P<0.05$) compared to that quantified in control seedlings (0.41 g Kg^{-1}) with the imposition of 10 bends (0.65 g Kg^{-1}) and 40 daily bends (0.57 g Kg^{-1}). However, when analyzing the content in the element, it can only be observed that with the imposition of 20 bends per day, there was a reduction in the element. Therefore, *G. ulmifolia* seedlings subjected to 10 and 40 daily bends concentrated more of the element at the expense of less biomass allocated to the stem tissues.

Table 1. Concentration (T) and content (C) of nitrogen (N) from stem (S) and roots (R) of *Guazuma ulmifolia* seedlings as a function of stem bending frequency.

	TNS	**TNR**	**CNS**	**CNR**
	----- g Kg^{-1} -----		**----- g per plant -----**	
0	0.41 b	0.69 a	0.46 a	0.65 a
10	0.65 a	0.66 a	0.43 a	0.63 a
20	0.40 b	0.50 b	0.30 b	0.46 b
40	0.57 a	0.66 a	0.47 a	0.50 b
CV (%)	6.8	5.0	6.9	5.2
$W_{p\text{-value}}$	0.28	0.91	0.14	0.97
$B\text{-}F_{p\text{-value}}$	0.27	0.07	0.45	0.11

Averages followed by the same lowercase letter in the column do not differ significantly from each other according to the Tukey test at a 5% probability of error. In which: CV: coefficient of variation; $W_{p\text{-value}}$: probability of significance of normality of distribution of experimental errors; $B\text{-}F_{p\text{-value}}$: probability of significance of homogeneity of variances of experimental errors.

Regarding the root system (Table 1), it was observed that N was significantly lower only with 20 bends, indicating that the stress suffered led to lower absorption of the element, given that the root biomass was not significantly altered at this intensity and the N content detected was significantly lower than in the control treatment. Additionally, the low content observed in stem tissues corroborates this behavior. For seedlings exposed to 40 daily bends, lower root biomass was observed, resulting in lower N content in the organ, without, however, any differences in the content measured in the root system.

Nitrogen (N) is considered an essential element for terrestrial plants, as it is present in the composition of the most important biomolecules such as ATP, NADH, NADPH, chlorophyll, proteins, and numerous enzymes. Nitrogen is the mineral nutrient proportionally most required by terrestrial plants (SOUZA & FERNANDES 2018). Due to greater investment in aerial growth (HOUMANI & CORPAS 2024), it is common for there to be greater nutritional demand for that plant system. Of all the nutritional elements in higher plants, nitrogen is generally found in the highest concentrations. In superior plants, nitrogen is part of proteins, nucleic acids, and other important cellular constituents, including membranes and various plant hormones.

Under abiotic stress, the capacity and efficiency in reconfiguring various metabolic networks is a determining factor in plant acclimatization. This adaptive response involves communication between root and aerial tissues with regard to different long-distance signaling molecules, including nutrients, hormones, assimilates, and peptides (HOUMANI & CORPAS 2024).

With regard to phosphorus (Table 2), it can be seen that when applying an intensity of 10 stem bends, there is a higher content and accumulation of the element in the root tissues, whereas in the stem tissues, despite there being a higher content of the element, the content is relatively low given the lower biomass. It should also be noted that seedlings subjected to 20 daily stem bends preferentially allocate the element to the root system, given that in aerial tissues, the content and concentration are significantly lower than in other treatments.

It should be noted that recognition of the stressor imposed by 10 stem bending tests resulted in a higher demand for that nutrient by the plant, as levels increased by 40% and 29% in both stem and root tissues, respectively, compared to those detected in control seedlings. With an increase of more than 10 bends per day, the detected levels decreased, indicating acclimatization to the stressor.

Table 2. Concentration (T) and content (C) of phosphorus (P) from stem (S) and roots (R) of *Guazuma ulmifolia* seedlings as a function of stem bending frequency.

Frequency of stem bend	TPS	TPR	CPS	CPR
	----- g Kg^{-1} -----		----- g per plant -----	
0	2.03c	1.59 b	2.24 a	1.50 b
10	2.84 a	2.05 a	1.88 c	1.95 a
20	1.87 d	1.49 b	1.41 d	1.39 b
40	2.45 b	1.61 b	1.99 b	1.22 c
CV (%)	2.8	3.5	2.6	3.4
$W_{p\text{-value}}$	0.47	0.40	0.52	0.13
$B\text{-}F_{p\text{-value}}$	0.12	0.41	0.12	0.41

Averages followed by the same lowercase letter in the column do not differ significantly from each other according to the Tukey test at a 5% probability of error. In which: CV: coefficient of variation; $W_{p\text{-value}}$: probability of significance of normality of distribution of experimental errors; $B\text{-}F_{p\text{-value}}$: probability of significance of homogeneity of variances of experimental errors.

The lack of phosphorus (P) in most tropical soils is a limiting factor for the growth of exotic and native woody species (FURTINI NETO et al. 1999). Phosphorus is an essential element in plant metabolism, fundamental in cell energy transfer, respiration, and photosynthesis. Phosphorus deficiency in substrates causes irregular growth, both in the aerial part and in the root system, impairing the quality of seedlings (GOMES & PAIVA 2012).

Phosphorus also acts as a signaling molecule for hormone synthesis. According to its internal concentration, phosphorus stimulates ethylene synthesis, which consequently modulates the development of secondary roots, root hairs, and lignin biosynthesis, in addition to inhibiting primary root growth (WANG et al. 2021). When the phosphorus content in the root system is high, meristematic activity is attenuated, decreasing cell division, which compromises root growth. This physiological response is activated via increased ethylene production in that organ (SHUKLA et al. 2017).

Plants invest in different defense strategies against stressors, which are triggered during the stress recovery phase and involve anabolism for direct defense against stressors, such as biosynthesis for physical barriers or even repellent responses (MACEDO 2012). *G. ulmifolia* is a species with high pharmacological potential, and among its identified compounds are those associated with defense metabolism. The most representative are the contents of terpenoids, flavonoids, phenolic compounds, tannins, and alkaloids, compounds that are associated with plant defense responses (PRAHASTUTI et al. 2020, RAFI et al. 2020).

These compounds, like terpenoids, require phosphorus in their constitution, in the biosynthetic pathway of mevalonic acid (TAIZ et al. 2017). Therefore, the mechanical stimulus induced by 10 daily bends may signal the activation of this pathway, causing phosphorus to be required in higher concentrations, whereas increasing the intensity of daily bends decreases this demand, indicating exhaustion from injury, leaving the plant more susceptible and culminating in metabolic collapse.

The potassium content in the stem tissues was not affected by the frequency of stem bending (P>0.05). However, given the lower biomass observed in seedlings that suffered mechanical injury, the contents were significantly lower compared to the control treatment (Table 3), while in the root system, the frequencies of 10 and 20 daily bends resulted in a lower content in this organ. It should also be noted that even though they had statistically the same biomass, the contents were lower than those of the control treatment.

Lower potassium (K) values may be associated with the integrity of the root system's biological membranes, as measured by the REE test. The greater overflow with the increase in caudal bending frequencies indicated that this nutrient was not fully absorbed into the plant cell, but was acting to maintain the electrochemical potential of the biological membranes of the root system, in the active transport of nutrients such as calcium and magnesium, as well as acting synergistically in the absorption of phosphate in the root system.

Table 3. Concentration (T) and content (C) of potassium (K) from stem (S) and roots (R) of *Guazuma ulmifolia* seedlings as a function of stem bending frequency.

Frequency of stem bend	TKS	TKR	CKS	CKR
	----- g Kg^{-1} -----		----- g per plant -----	
0	12.12 a	20.19 a	13.39 a	18.72 a
10	8.23 a	11.59 b	5.45 c	11.56 bc
20	11.64 a	8.28 b	8.78 b	7.98 c
40	10.89 a	17.3 a	8.85 b	12.99 b
CV (%)	26.5	17.4	29.4	17.2
$W_{p\text{-value}}$	0.41	0.27	0.58	0.41
$B\text{-}F_{p\text{-value}}$	0.71	0.96	0.66	0.92

Averages followed by the same lowercase letter in the column do not differ significantly from each other according to the Tukey test at a 5% probability of error. In which: CV: coefficient of variation; $W_{p\text{-value}}$: probability of significance of normality of distribution of experimental errors; $B\text{-}F_{p\text{-value}}$: probability of significance of homogeneity of variances of experimental errors.

Under stress conditions, potassium is retained and accumulated in the cytosol of plant cells, acting as a signal for gene expression of the antioxidant machinery and for the biosynthesis of defense compounds (HOUMANI & CORPAS 2024). However, in an attempt to maintain the electrochemical potential of membranes, potassium began to be reabsorbed, increasing its content, as observed in root tissues with an intensity of 40 stem bends (Table 3).

The absence of K can result in restricted photosynthesis, chlorosis followed by necrosis, and reduced growth (RAIJ 1991). Element K has no structural function, but is associated with greater resistance in plants when subjected to adverse conditions, such as low water availability and extreme temperatures, due to its role in the opening and closing of stomata (KERBAUY 2013). Therefore, K deficiency reduces plant tolerance to water deficit via prevention and adaptation to stress (TRÄNKNER et al. 2018).

Of all mineral nutrients, potassium (K) plays a particularly critical role in plant growth and metabolism, contributing to survival under various abiotic stresses. K is an essential nutrient and the most abundant cation in higher terrestrial plants. The concentration of K^+ within the cytoplasm was consistently found to be between 100 and 200 mM (SHABALA & POTTOSIN 2010), while the apoplastic K^+ concentration can vary between 10 and 200 or even reach up to 500 mM (WHITE & KARLEY 2010).

The main functions that K^+ performs in higher terrestrial plants include enzymatic activation, active participation in establishing cell turgor and maintaining cell electro-neutrality, as well as being involved in photosynthesis, carbohydrate transport, protein synthesis, cell expansion, and stomatal movement (TAIZ et al. 2017).

The calcium (Ca) content in the stem (Table 4) increased with 20 stem bends (9.07 g Kg^{-1}) when compared to the content determined in control seedlings (6.70 g Kg^{-1}). However, even though there was an increase in the content of the element in the stem tissues, there appears to be a concentrating effect of the element, since the content was statistically equal to that observed in control seedlings, while the content observed in the root system was similar to that observed in the dry root biomass (Figure 1a).

Calcium is considered a basic element in the acid-base balance of plants, and any alteration in this balance impairs or slows growth. Additionally, it alters the shape of plant tissues, reducing root formation and delaying both flowering and fruiting, constituting an important component of cell wall integrity.

Table 4. Concentration (T) and content (C) of calcium (Ca) from stem (S) and roots (R) of *Guazuma ulmifolia* seedlings as a function of stem bending frequency.

Frequency of stem bend	**TCaS**	**TcaR**	**CCaS**	**CCaR**
	----- g Kg^{-1} -----		**----- g per plant -----**	
0	6.70 b	6.02 a	7.41 a	5.67 ab
10	8.34 ab	6.48 a	5.52 b	6.15 a
20	9.07 a	6.83 a	6.83 a	6.38 a
40	8.68 ab	6.90 a	7.06 a	5.24 b
CV (%)	11.2	6.4	12.1	6.6
$W_{p\text{-value}}$	0.92	0.95	0.46	0.82
$B\text{-}F_{p\text{-value}}$	0.08	0.96	0.09	0.97

Averages followed by the same lowercase letter in the column do not differ significantly from each other according to the Tukey test at a 5% probability of error. In which: CV: coefficient of variation; $W_{p\text{-value}}$: probability of significance of normality of distribution of experimental errors; $B\text{-}F_{p\text{-value}}$: probability of significance of homogeneity of variances of experimental errors.

The magnesium (Mg) content in the stems of *G. ulmifolia* seedlings increased (Table 5) with all frequencies of stem bending (average of 2.42 g kg^{-1}) compared to the value obtained from the stems of control seedlings (1.76 g kg^{-1}). With increased concentration and given the lower biomass, the Mg content in the stems was not significantly altered.

The increase in magnesium content in the stem may be in response to mechanical stress imposed by stem bending. Mechanical stress increases the respiratory activity of plants to sustain a variety of physiological effects (KOUHEN et al. 2023). Magnesium acts as a cofactor for many phosphorylating enzymes, forming a bridge between ATP or ADP pyrophosphate and the enzyme molecule, with energy transfer being essential for photosynthesis and respiration processes in organic compound synthesis reactions, ionic absorption, and mechanical work performed by the plant (LIMA et al. 2018).

The magnesium content in the root system decreased with 20 and 40 stem bends and appears to be associated with the phosphorus content observed in the root system. Magnesium acts as a phosphorus carrier in plants, meaning that phosphorus absorption would be greater in the presence of magnesium, given its importance in phosphorylation reactions (LIMA et al. 2018). According to SOUZA et al. (2009), the omission and low requirement of Mg in the initial propagation phase contributed to the formation of pink cedar seedlings with larger collar diameters compared to the control seedlings.

Table 5. Concentration (T) and content (C) of magnesium (Mg) from stem (S) and roots (R) of *Guazuma ulmifolia* seedlings as a function of stem bending frequency.

Frequency of stem bend	TMgS	TMgR	CMgS	CMgR
	----- g Kg^{-1} -----		----- g per plant -----	
0	1.76 b	1.95 a	1.94a	1.84 a
10	2.58 a	1.89 a	1.71a	1.80 ab
20	2.47 a	1.32 b	1.86a	1.23 c
40	2.20 a	1.79 ab	1.79a	1.36 bc
CV (%)	8.2	13.0	8.3	13.2
$W_{p\text{-value}}$	0.15	0.73	0.14	0.45
$B\text{-}F_{p\text{-value}}$	0.86	0.58	0.81	0.55

Averages followed by the same lowercase letter in the column do not differ significantly from each other according to the Tukey test at a 5% probability of error. In which: CV: coefficient of variation; $W_{p\text{-value}}$: probability of significance of normality of distribution of experimental errors; $B\text{-}F_{p\text{-value}}$: probability of significance of homogeneity of variances of experimental errors.

Growing evidence suggests that mineral nutrients play a critical role in the resistance of woody terrestrial plants to stresses (MARSCHNER 2012). The production of resistant seedlings, capable of surviving and tolerating abiotic adversities, is one of the possible alternatives to minimize post-planting mortality, especially water deficit.

The cultural and silvicultural practices used in nurseries have a strong influence on the performance of seedlings immediately after planting in the field (RIIKONEN & LUORANEN 2018). Several authors have indicated that mechanical stimuli, irrigation cycles, and the application of plant growth regulators have had beneficial results in the adaptation of woody species seedlings to post-planting stress (VILLAR-SALVADOR et al. 2004, JACOBS & LANDIS 2009, CADORIN et al 2021).

The hardening or acclimatization techniques imposed on the seedlings in this trial did not result in stress, as indirectly assessed by the REE test results. The REE test consists of quantifying ions that have leaked through the cell membrane into the solution and can even be non-destructive, as it uses a sample of roots. Under stressful conditions, cell membranes lose their selective permeability and consequently their ability to retain ions. Therefore, quantifying the ions that leak through the cell membranes of root tissues estimates the conditions of their cellular integrity (DRANSKI et al. 2017, KOVALESKI & GROSSMAN 2021).

Hardening off using stem bending has shown promising results in seedling quality and initial performance after planting. VOLKWEIS et al. (2014) observed in *Maytenus ilicifolia* seedlings that stem bending imposed as a hardening strategy promoted morphophysiological changes that increased the hardiness and quality of seedlings suitable for planting. DRANSKI et al. (2015) reported that *Pinus taeda* seedlings hardened by stem bending showed faster growth in height and collar diameter 90 days after planting, while CADORIN et al. (2015) reported better performance after 180 days of planting in *Cordia trichotoma* seedlings, measured by growth rate in height and collar diameter compared to seedlings that were not mechanically stimulated.

Due to the pioneering aspect of the species in terms of its photochemical and mechanical acclimatization capacity, associated with its ability to colonize environments with alkaline and low-fertility soils, hardened mutamba seedlings with stem bends deserve to be tested in revegetation projects.

CONCLUSION

The frequencies of stem bending altered the allocation of macronutrients in the stem and roots of *Guazuma ulmifolia* seedlings, resulting in increased concentrations of nitrogen, phosphorus, calcium, and magnesium in the stem tissues, while in root tissues, there was an increase in phosphorus content and a reduction in potassium content in order to maintain satisfactory growth rates with the increase in stem bending intensity.

Therefore, the results of this research contribute to the understanding of the species' competitive and colonization capacity in disturbed environments, which can support future ecological restoration strategies, with the choice of species and their propagation protocol in nurseries.

AUTHORS' CONTRIBUTIONS

UCM **c**onceptualization, supervision, methodology, revision, and editing
MA research, formal analysis, preparation of original manuscript, revision, and editing
MCL revision and editing
JAD formal analysis, review, and editing
All authors have read and agreed to the published version of the manuscript.

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CONFLICT OF INTEREST

There is no conflict of interest.

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